THE INFLUENCE OF SIZE DIFFERENTIAL ON AGONISTIC ENCOUNTERS BETWEEN INTERMOULT FRESHWATER CRAYFISH IN *CHERAX CUSPIDATUS* RIEK, 1969 (DECAPODA: PARASTACIDAE)

The resource holding potential (RHP, Parker 1974) of an animal is a measure of that individual's absolute fighting ability, and consists of a combination of its morphological and physiological traits such as body size, age, size of weapons, armour and energy reserves (Caldwell, 1987). RHP is one of several concepts generated from the application of game theory to animal contests (Maynard Smith and Parker, 1976; Parker and Rubenstein, 1981). Such concepts have enabled the formulation of testable predictions relating to the agonistic behaviour of animals under various contest conditions.

The research outlined in this paper tested two predictions of simple game theoretic models. These were:

1. an asymmetry in RHP between opponents will decide contest outcome; and

2. RHP differences between opponents will determine strategies used in contests, with escalated interactions likely to occur between opponents with similar RHP.

Methods

Sexually immature, intermoult, young of freshwater crayfish *Cherax cuspidatus* were used in experiments. Total carapace length (T.C.L.) was the RHP index employed. Crayfish were paired at five size ratios : 1:1, 1:0.9, 1:0.8, 1:0.7 and 1:0.6 and allowed to interact for 180 minutes in containers (9 x 9.5 x 9.5cm high) with no shelter present. Crayfish were released into the containers simultaneously to eliminate any possible ownership effect. Replication level was 16.

The initiator, winner, duration and type (whether fight, attack, strike or threat) of each agonistic interaction was recorded. The dominant individual for each pair was defined as the one which won at least 60% of all interactions. The size of each dominant (whether the larger or smaller member of the pair) was also recorded.

Results and Discussion

The larger animal was always dominant once the size difference was 20% or more. The larger individual was dominant significantly more often than expected by chance at the 1:0.9 ($p<0.01$) and 1:1 ($p<0.05$) size ratios. Two pairs at the 1:1 ratio had equal T.C.L. values. The remainder was separated by differences between 0.85 and 4.05%, indicating that size discrepancies of less than 5% can influence outcome of agonistic interactions.

The measurements taken for the four pairings at 1:1 and three at 1:0.9 in which the individual with smaller T.C.L. was dominant, revealed that in each case the 'smaller' animal was superior in at least one of the other potential RHP values (weight, chelae length, age). This result suggests that a single RHP index has limited utility for pairs when both members are superior in one or more morphological measurements. Such a situation is especially relevant to organisms with indeterminate growth, e.g. Crustacea.

Size discrepancy between opponents had a significant inverse relationship with total agonistic time, fight time, maximum and average bout length ($p<0.001$), fight frequency and frequency of all interactions ($p<0.01$), and strike frequency and time of threat, strike and attack combined ($p<0.05$). Attack frequency, threat frequency and attack response latency did not vary significantly between size ratios.

Size discrepancy had an inverse relationship with the proportion of interactions initiated by the smaller animal in each replicate ($p<0.05$), but formed no significant relationship with proportion of interactions won by the smaller individual ($p>0.05$). The larger animal in each pair initiated ($p<0.01$) and won ($p<0.0001$) the first agonistic interaction significantly more often than expected by chance. The smaller animal initiated a proportion of the first interactions, irrespective of size ratio.

Assessment of RHP among pairs of *C.cuspidatus* always involved agonistic interaction, possibly as a means to probe for recently moulted crayfish. Differences in RHP between opponents determined the outcome of interactions. Contests in which opponents could accurately assess the asymmetry in RHP, i.e. 1:0.6 and 1:0.7 size ratios, were settled without escalation. Those in which role assessment could not be accurately made by conventional behaviour, i.e. 1:1, 1:0.9, 1:0.8, resulted in escalation. The results of this work are in agreement with the predictions generated by simple game theoretic models.

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